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EXAMPLES OF ORTHOGENETIC SERIES IN PLANTS AND ANIMALS

STUDIES IN DETERMINATE EVOLUTION X*

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Orthogenetic series are so prominent in both the plant and animal kingdoms that their consideration becomes of major significance in any careful study of the evolution of organisms. A few types of plant series are here presented together with several animal series in order to illustrate the nature and significance of orthogenesis. In studying living organisms one cannot tell directly, from the orthogenetic series itself, what is the real relationship of the members of a series to one another nor in what sequence they evolved; but this is after all of secondary importance. The fundamental problem is the fact that the evolutionary process brings out such a series and that these series usually have no relation either to utilitarian advantage or to any ecological conditions either physical or biological. The evolution of each series is commonly independent of other movements in the same group of organisms and may even proceed in a different direction or in a sequence exactly the opposite. In the past the most definite orthogenetic series were recognized in the fossil records and in these, of course, the direction of any given movement or sequence was definitely indicated by the succession of the rock strata in which the fossils were found.

In attempting to explain orthogenetic series in the past it was usually assumed that the series was the result of natural selection or was produced by ecological sequences, either in time or space by a direct effect of the environment. However, any one who has only a superficial knowledge of orthogenetic series and their taxonomic relations soon discovers that they

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have no general correspondence with any ecological gradations, whether considered from the standpoint of the Darwinian survival of the fittest, of a direct response to environment, or of a fancied Lamarckian use or disuse. Most of the series are found to lie entirely outside of any possible teleological implications, and have no more to do with advantageous or utilitarian determination than have the many interesting series of molecules often met with in organic chemistry or the various series of forms and patterns appearing in certain types of crystallization.

Recently certain geneticists have attempted to resurrect the natural selection corpse and to develop a new type of evolutionary theory based on the fortuitous mutations of genes and a utilitarian selection. But this genetic hypothesis is again entirely beside the mark, for it does not touch the fundamental problems of the taxonomic system nor the taxonomic series with which the systematist has to deal. No simple external physical agent postulated as a fundamental cause of evolution, as X-rays, cosmic rays, ultra-violet rays, etc., can receive any serious consideration from any biologist who has some general knowledge of the organic kingdom; because it is evident that it is impossible logically to depend on random and universal agents, like the various radiations, to account for the fundamental fact of orthogenetic series when these series show no zonal arrangement in relation to supposed causal agents. It is a well-known fact that in ecological zonation of plants there can be, and usually is, a haphazard assemblage of diverse taxonomic types in the same zone which in itself shows that the taxonomic structures have neither been produced as a result of the environment nor been arranged in the zones because of taxonomic relation.

Any theory of evolution worthy of the consideration of any serious-minded biologist must also take account of the fundamental biological realities which go much deeper than the mere matter of speciation.

ORTHOGENETIC SERIES IN PLANTS

One of the decided and oft-repeated orthogenetic series to be observed in the flower is the progressive reduction of the floral members until the determinate limit is approached or reached for some essential organ. In the Alismatales, for example, *Echinodorus radicans* (Nutt.) Engelm. has about 20 stamens; species of *Lophotocarpus* have 15–9; *Helianthium*

parvulum (Engelm.) Small has 9; *Alisma plantago* L. has 6; *Potamogeton* species have 4; *Ruppia maritima* L. has 2; *Zannichellia palustris* L. and species of *Naias* have but a single stamen in the staminate flower. In this series the progression is to completely submerge plants and hydrophilous pollination, from an aerial habitat and entomophilous pollination. Now, in the anemophilous, aerial grasses, most of the bamboos have 6 stamens or sometimes even more to the flower; *Arundinaria* and the lower herbaceous grasses have 3, *Andropogon scoparius* Mx. has 3, *Andropogon elliottii* Chapm. has 1. Various entomophilous groups show the same sequence. In the Orchidales, *Thismia* has 6 stamens, *Neuwiedia* 3, *Cypripedium* 2, *Arethusa* and hundreds of other orchid genera have 1. In the Scitamimales, *Ravenala* has 6 stamens, *Musa* sp. 5, *Hedychium* and *Alpinia* 1, *Canna* and *Maranta* have only a half fertile stamen in the flower. Such series appear in numerous other monocotyl groups. Thus it will be seen that whether the plants pass under the water or remain in aerial conditions, whether the flowers are bisporangiate or monosporangiate, whether pollination is hydrophilous, anemophilous, or entomophilous, the results are the same in the evolutionary series in so far as the stamens are concerned. Neither the series as a whole nor any special member of the series shows any relation to the environment nor any advantage or disadvantage of one type over another. All of these species with one or with a half stamen are successful. There is no such thing as adaptation or utility in evidence as having any causal relation to the series. The same condition of things is evident in many lines of dicotyls. Taking for example a common dry land weed series in the Centrospermae: *Agrostemma githago* L. has 10 stamens, *Alsine media* L. 10–2, *Chenopodium album* L. 5, *Chenopodium rubrum* L. 2–1, *Monolepis nuttalliana* (R. & S.) Greene 1.

In certain groups the embryos of various species make a progressive series from straight to very decidedly coiled. A series in which the embryos develop under water is as follows: *Naias flexilis* (Willd.) R. & S. embryo straight, *Potamogeton heterophyllus* Schreb. embryo curved, *P. compressus* L. embryo slightly spiral, *P. diversifolius* Raf. embryo coiled, *P. dimorphus* Raf. embryo spirally coiled. This series may be compared with a series of common weeds of dry fields: *Polygonella americana* (F. & M.) Small, embryo straight or nearly so, *Rumex* sp. embryo slightly curved; *Polygonum* sp. embryo curved; *Cheno-*

podium ambrosioides L. embryo curved in an incomplete ring; *C. album* L. embryo forming a complete ring; *Sarcobatus vermiculatus* (Hook) Torr. embryo coiled into a flat spiral; *Salsola pestifer* Nels. embryo coiled into a conic spiral. The degree of coiling has neither significance of advantage or disadvantage in itself nor in relation to the environment. The two series occur in the two most extremely diverse ecological conditions imaginable. No "natural selection" nor utilitarian response to the environment had anything to do as a causal agent with the result.

Various monocotyl groups show a progressive union of the perianth segments. In *Aloe haworthioides* Bak. and *A. pratensis* Bak. the perianth segments are entirely free; in *A. myriacantha* (Haw.) R. & S. the perianth segments are only slightly united at the base; in *A. chloroleuca* Bak. the segments are united about one-fourth; in *A. somaliensis* C. Wright they are united about one-third; in *A. rubrolutea* Schinz the segments are united one-half; in *A. shimperi* Todaro they are united two-thirds; in *A. marshallii* W. & E. they are united three-fourths; and in *A. leptophylla* N. E. Brown the perianth segments are united more than four-fifths of their length. Nearly all of these species are South African.

In the Eriocaulaceae, there is a characteristic orthogenetic series in the change from ordinary petals to petals changed to a pappus or mass of hairs. This series is well represented by the petals of the carpellate flowers of the following species: 1, *Eriocaulon guianense* Koern.; 2, *E. longifolium* Nees.; 3, *E. crassiscapum* Bong.; 4, *E. woodii* N. E. Br.; 5, *E. majusculum* Ruhl.; 6, *E. griseum* Koern.; 7, *Lachnocaulon anceps* (Walt.) Morong. The extreme forms give an unusual type of flower with the petals represented by hairs between the calyx and gynecium. The sepals may also be similarly affected; but usually to a much less degree than the petals.

A common character in many genera of grasses is the presence of an awn on the lemma. These awns are of various lengths from mere points to structures of decided prominence. Thus in the genus *Bromus* the following series is to be observed: *B. inermis* Leyss has no awn; in *B. unioloides* (Willd.) H. B. K. the lemma has an awnpoint less than 1 line long; *B. kalmii* Gr., awn 1–1½ lines long; *B. purgans* L., awn 2–3 lines; *B. asper* Murr., awn 3–4 lines; *B. secalinus* L., awn 4 lines but sometimes awnless; *B. patulus* M. & K., awn 4–5 lines; *B. sterilis* L.,

awn 6–9 lines. A number of species of *Agrostis* in eastern North America have awns as follows: *A. perennans* (Walt.) Tuck. has no awn on the lemma; *A. hyemalis* (Walt.) B. S. P., sometimes awnless, sometimes with a very short awn; *A. geminata* Trin., awn 1 line long or less; *A. canina* L., exserted awn 1–2 lines; *A. borealis* Hartm., awn 2–2½ lines; *A. elliottiana* Schultes, awn 3–4 lines. *Festuca*, *Elymus*, *Muhlenbergia*, *Oryzopsis*, and *Andropogon* present similar conditions. Why these various specific lengths of these appendages? They are of no advantage or disadvantage. The species without awns are just as successful as those with awns; the short-awned species are just as good as the long-awned. But the orthogenetic series is definitely present and it must be considered without any fantastic hypothesis of teleological adaptation. To claim that such structures are of selective value presents the height of philosophical credulity; to see in them a response to environment is equally absurd. Nevertheless the evolutionary process is such that awns are evolved in the various species and these awns appear in various lengths, making the orthogenetic series.

The pods in the Brassicales are sometimes sessile and sometimes stalked. The stalks are also developed in various lengths. Brassicaceae—*Alliaria alliaria* (L.) Britt. has the pod sessile in the calyx; *Thelypodium integrifolium* (Nutt.) Endl., pod short-stipitate; *Stanleya pinnata* (Pursh) Britt., pod long-stipitate. Capparidaceae—*Polanisia graveolens* Raf., pod sessile in the calyx; *Cristatella jamesii* T. & G., stalk of pod 2 lines long; *Cleomella angustifolia* Torr., stalk of pod 3–4 lines; *Cleome serrulata* Pursh, stalk of pod 6–8 lines; *Cleome spinosa* L., stalk of pod 2–6 inches long.

In the evening primrose family as well as in some other groups, the epigynous hypanthium develops from nothing up to 7 inches or more in length. The following represents a series of various lengths: *Jussiaea* and *Chamaenerion* have no hypanthia; *Kneiffia linifolia* (Nutt.) Spach., hypanthium less than ¼ in. long; *Kneiffia longipedicellata* Small, hypanthium ½ in.; *Oenothera oakesiana* Robb., hypanthium 1 in. long. *Oenothera biennis* L., hypanthium up to 1½ in long; *Taraxia breviflora* Nutt., hypanthium up to 2 in. long; *Pachylophus canescens* Piper, hypanthium 3 in. long; *Oenothera longissima* Rydb., hypanthium 4 in. or more long; *Megapterium missouriense* (Sims) Spach, hypanthium up to 6 in. long; *Pachylophus caespitosa* (Nutt.) Rain., hypanthium up to 7 in.

long. A similar condition is represented by species of the Amaryllidaceae. *Leucojum vernum* L. has no perianth tube; in *Lophiola americana* (Pursh) Cov. the perianth segments are slightly united at the base; *Narcissus pseudo-narcissus* L. has a definite hypanthium ½ in. long; *Narcissus odorus* L., hypanthium ¾ in.; *Narcissus poeticus* L., hypanthium 1 in.; *Cooperia drummondii* Herb., hypanthium 1½ in.; *Hymenocallis occidentalis* (LeC.) Kunth, hypanthium 2 in.; *Crinum asiaticum* L., hypanthium 2¾ in.; *Hymenocallis macrostephana* Bak., hypanthium 3 in.; *Crinum amabile* Don., hypanthium 4 in.; *Hymenocallis kimballiae* Small, hypanthium 6½ in.; *Hymenocallis collieri* Small, hypanthium up to 7½ in. long. Again we see a gradation series of lengths in the same genus or closely related genera and in the same general environment. The moths, butterflies, and other insects get nectar from these tubes provided they have a proboscis or tongue long enough to fit the given case or can tear the tube open. But whether they obtain nectar or not, the mere act of alighting on the flower will induce pollination, since the stigmas and anthers are at approximately the same level above the tube of the hypanthium. Moths could survive because as the orthogenetic process brought out all sorts of lengths of probosces in the insects a similar orthogenetic movement was bringing out endless sorts of flowers with longer or shorter tubes, and it is evident that a moth with a long proboscis can very readily sip nectar from a flower with a very short tube as well as from one with a long tube. These orthogenetic series of nectar tubes have no significance in survival. To indulge in fantastic teleological speculations in respect to these developments does not explain why the whole orthogenetic series survived nor the fact that many flowers without nectar tubes or nectar are still visited by numerous insects bent on gathering pollen.

The Orthogenetic Series in the evolution of the solid or adnate hypanthium in Iris shows conclusively that the hypanthium in Iris was not produced as a "special adaptation" to prevent "unbidden guests" from pilfering the nectar reserved for moths with long probosces. The nectar is at the top of the solid hypanthium in this case.

1. *Iris xiphium* L. has no hypanthium. 2. *I. sibirica* L. has a tubular hypanthium ⅛–¼ in. long with no solid lower portion. 3. *I. ensata* Thunb. has a hypanthium ¼ in. long, the lower ⅛ in. being solid. 4. *I. versicolor* L. and *I. pseuda-*

corus L. have hypanthia about ½ in. long, ¼ in solid, and ¼ in tubular. 5. *I. chamaeiris* Bertol. has a hypanthium 1 in. long. 6. *I. cristata* Ait has a hypanthium 2¾ in. long, the solid portion being 2½ in. and the upper tubular portion ¼ in. 7. *I. reticulata* Bieb. has a hypanthium 3 in. long. 8. *I. unguicularis* Poir. has a hypanthium up to 6 in. long.

In addition to developing hypanthia, the species of Narcissus evolved a new structure, the crown, on top of the hypanthium. Since this is a new morphological structure, the evolutionary movement also brings out crowns of various lengths in an orthogenetic series independently of the length of the hypanthia on which they develop. *Crinum asiaticum* L. has no sign of a ridge or crown on the top of the hypanthium; *Narcissus jonquilla* L. has a short crown not over ⅛ in. long; *N. triandrus* L., crown ¼–½ in.; *N. pseudo-narcissus* L., wild variety, crown 1 in. long, cultivated varieties, crown up to 2 in. long. All the many species and varieties of *Narcissus* have crowns ranging within this series.

In the Ranunculaceae, various genera develop nectar pits or spurs on the petals, while other quite similar genera have no pits or spurs. The nectar spurs are prominent in *Aquilegia*. Just as in the case of length of awns or length of hypanthia these nectar spurs form an orthogenetic series. In the genus *Anemone* there are no nectar pits on the perianth segments. *Myosurus minimus* L. and species of *Ranunculus* have small pits at the base of the petals about 1 line deep; *Heleborus viridis* L. has petal tubes 2 lines deep; *Aquilegia eastwoodiae* Rydb. has the petals merely saccate, not spurred; *A. brevistyla* Hook. has nectar spurs about 3 lines long; *A. glandulosa* Fisch., nectar spurs 3–6 lines; *A. sibirica* Lam., nectar spurs 6–9 lines; *A. canadensis* L., nectar spurs 8–10 lines; *A. formosa* Fisch., nectar spurs 9–12 lines; *A. skinneri* Hook., nectar spurs 1½–2 in.; *A. chrysantha* Gr., nectar spurs 2–2½ in. long; *A. longissima* Gr. has a spur 5 in. long. As in the evening primrose, the pollination does not depend on whether the insect can reach the nectar in the bottom of the spur. If the insect alights on the flower, pollination will be accomplished. In this connection one may recall the fantastic notions of "favored and unbidden guests." I have seen bumblebees and honeybees attempting to get at the nectar of the long-spurred columbines without success, but in the meantime pollination was accomplished as readily as if a long-proboscis hawkmoth had hovered over the flowers and sipped the cup of nectar.

One meets with orthogenetic, perfection series in many different types of structure. The glandular pits on the backs of the leaves of species of *Cupressus* show such a series. *Cupressus goveniana* Gord. has glandless leaves; *C. macrocarpa* Hartw. has the leaves glandless or obscurely pitted; *C. guadalupensis* S. Wats., leaves with a dorsal pit but not resin-glandular; *C. macnabiana* Murr., leaves with a conspicuous gland on the dorsal surface secreting resin; *C. glabra* Sudw. leaves with a very conspicuous resin-secreting gland on the back.

There is an orthogenetic series in relation to those extraordinary developments, the pollinia, in the Orchidales. *Thismia hyalina* (Miers) B. & H. has round, smooth pollen grains of the ordinary type. In the main subfamily of Orchids, the Orchidatae, *Cephalanthera grandiflora* (Scop.) Bab. also has granular pollen of the ordinary type. *Arethusa bulbosa* L. has powdery-granular pollen; *Corallorrhiza wisteriana* Conrad, pollinia soft waxy without a caulicle; *Liparis liliifolia* (L.) Rich., pollinia two in each anther sac smooth and waxy, in pairs slightly united but without a stalk, thread, or gland; *Tipularia unifolia* (Muhl.) B. S. P., pollinia ovoid, two in each anther-sac, separate, affixed to a short stipe which is glandular at the base; *Coeloglossum bracteatum* (Willd.) Parl., pollinia oblong-ovoid, with a long caulicle having a glandular base but scarcely wider than the caulicle; *Galeorchis spectabilis* (L.) Rydb., pollinia oblong, granulose, one in each anther-sac, with a slender caulicle having a large glandular disc at its base; *Lysias orbiculata* (Pursh) Rydb., pollinia with a prominent caulicle having an orbicular glandular disc at its base. Thus we see within the closely related plants of a single subfamily a closely graded perfection series of this extraordinary structure and the degree of perfection has nothing to do with survival of the species and there can be no selective action because the whole series is present from zero to the highly elaborated mechanism. In the Apocynaceae-Asclepiadaceae there is a somewhat similar progression from waxy pollen to the highly elaborated pollinia of Asclepias.

In the genus *Araucaria*, the widths of the leaves of the various species form an orthogenetic series from *A. araucana* (Mol.) Koch. with large broad leaves, thru *A. bidwillii* Hook. and *A. cunninghamii* Ait. to *A. excelsa* R. Br. with awl-shaped, vertically compressed leaves. Similar series occur in a number of other groups of Conifers. There is also a progressive series

of leaf widths in the *Populus-Salix* group from very broad to very narrow, as illustrated by the following species: *Populus deltoides* Marsh., *P. italica* Moench, *P. alba* L., *P. acuminata* Rydb., *Salix lucida* Muhl., *S. pentandra* L., *S. amygdaloides* And., *S. nigra* Marsh., *Populus angustifolia* James, *Salix interior* Row. The last two "mimic" each other very closely in size, shape, surface, and petiole length. Mimicries are the result of parallel or duplicate orthogenetic evolutions or sometimes of a mere accidental development of form, color, or structure, sometimes in closely related groups, sometimes in groups far apart in relationship, sometimes in the same geographic region, sometimes in regions widely separated. There is no evidence of "mimicry" in the old teleological sense. Such speculations, indulged in at great length by the older school of selectionists, were merely fantastic exercises of the imagination of the same scientific import as the imaginary designs of birth marks of fruits, leaves, seeds, plum pits, flames, etc., which the superstitious believe are caused by strong mental impressions of the mother during pregnancy. There is no more scientific evidence for a belief in selective mimicry than there is for the supposed prenatal influence of the mother's mind in determining birth marks.

In various groups there is an orthogenetic series in the development of the lobing of the petals, ranging from petals with rounded tips to very deeply divided petals. Such a series is present in the chickweed alliance as shown by the following: *Arenaria stricta* Mx., *A. hookeri* Nutt., *Cerastium semidecandrum* L., *Alsine holostea* (L.) Britt., *A. longipes* (Goldie) Cov., *A. media* L. (Fig. 1). Certainly no one with any knowledge of ecological relations would believe that any of these notched, lobed, or divided petals which make up the series are of any special advantage or environmental "adaptation."

The remarkable insectivorous leaf of *Drosera rotundifolia* L. has been widely exploited by teleologists. There is no question about its seemingly perfect "adaptation" for catching small insects. But when the genus is studied as a whole, *D. rotundifolia* is found to be but the end of an orthogenetic series, the preceding members of which, especially the first ones, are poorly fitted for catching insects. In fact the lowest are no more successful in this respect than great numbers of plants which have glandular or glutinous hairs or surfaces on the leaves or stems or in the inflorescence. A good series is represented by

the following species: *Drosera filiformis* Raf. with slender filiform leaves as the name implies; *D. linearis* Goldie, leaf blades linear; *D. longifolia* L., blades elongated spatulate; *D. intermedia* Hayne, blades short spatulate; *D. rotundifolia* L., leaf blades orbicular, abruptly narrowed into a flat, pubescent petiole. Thus it is seen that there are all degrees of this peculiar "adaptation" and that all have survived in their bog habitats. There has been no selection of the fittest at the expense of the less fit or the decidedly unfit in respect to the ability to catch insects. There has been no similarity in leaf form or perfective mechanism in relation to environment, but there has come out of the evolutionary process a very interesting orthogenetic series, and this series exists and calls for consideration no difference whether it evolved, step by step,

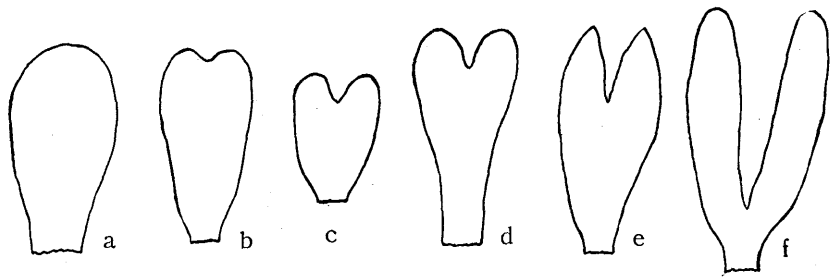

Fig. 1. Orthogenetic series in the division of the petal of closely related species in Caryophyllaceae. a, Entire petal of *Arenaria stricta* Mx. b, Slightly emarginate petal of *Arenaria hookeri* Nutt. c, *Cerastium semidecandrum* L. d, *Alsine holostea* (L.) Britt. e, *Alsine longipes* (Goldie) Cov. f, Divided petal of *Alsine media* L.

in the direction toward the perfected devise, or whether the members of the series mutated in an irregular manner. Finally it is doubtful whether there is any real advantage to the plant in the capturing of insects or other small creatures.

The evolution of the inflorescence also produces progressive series in many groups, as for example, in *Acer* and *Prunus*. *Acer pennsylvanicum* L. has a receme; *A. platanoides* L. a corymb; *A. saccharum* Marsh. an umbellate corymb; *A. saccharinum* L. an umbel-like cluster. *Prunus virginiana* L. has a raceme; *P. mahaleb* L. a corymbose inflorescence; *P. americana* Marsh. an umbel or fascicle; *P. spinosa* L. umbel reduced to 1–2 flowers.

One of the most peculiar and extreme types of fruits is the syconium or fig-fruit of the Common Fig, *Ficus carica* L.,

which represents a hollow or bottle-like, fleshy stem or inflorescence receptacle with the apex of the stem at the base of the cavity and with numerous flowers on the walls within. This type is a long distance away from the common type of fleshy ament as in species of *Morus*. In this case also the fig fruit does not represent a survival by selection or direct response to environment through the elimination of the less fit but is the end product of an evolutionary movement which produced another remarkable orthogenetic progression, practically all the general steps in the series being represented by living representatives. A few years ago it was the writer's good fortune to see a number of the species of the series in fruit at the Kew Gardens, England. The series may be illustrated by the following species: *Morus alba* L., *Dorstenia psilurus* Welw., *D. yambuyaensis* De Wild; *D. arifolia* Lam., *D. alata* Gardn., *Ficus carica* L. The fruit of *Dorstenia elata* Gardn. is a deep cup-like receptacle, while as is well known the fruit of *Ficus* has only a minute opening at the tip.

Various groups of plants show series of progressive flattenings of the stem and the development of two lateral wings from the ordinary cylindrical type. Such a series was outlined in a former paper of the "STUDIES." Extreme flattenings are represented by *Sisyrinchium grammoides* Bickn. and *Marica gracilis* Herb. belonging to the Iris Family. The genus *Lathyrus* of the Bean Family also shows species with progressive flattening of the stem with two wings as follows: *Lathyrus maritimus* L. and *L. venosus* Muhl. have the stem angled but not winged; *L. palustris* L. and *L. macranthus* (White) Rydb. have the angled stem slightly winged; *L. pusillus* Ell. and *L. grandiflorus* Sibth. and Sm. have the stem winged; *L. odoratus* L. has the stem prominently winged; *L. latifolius* L. has the stem broadly winged.

In various groups of Cacti there are progressive series from cylindrical to decidedly flattened stems, in the extreme types associated with a 2-ranked phyllotaxy. *Opuntia imbricata* (Haw.) Engelm., a tree Prickly-pear, has cylindrical stems; *O. fragilis* (Nutt.) Haw. joints somewhat flattened; *O. macrorrhiza* Engelm. joints decidedly flattened; *Epiphyllum oxypetalum* (DC.) Haw. (*Phyllocactus latifrons* Link) branches flat and thin, *Zygocactus truncatus* (Haw.) Schum., Christmas Cactus, joints exceedingly flattened and thin. In the genus *Ripsalis* there is a series of species from *R. virgata* Web. with

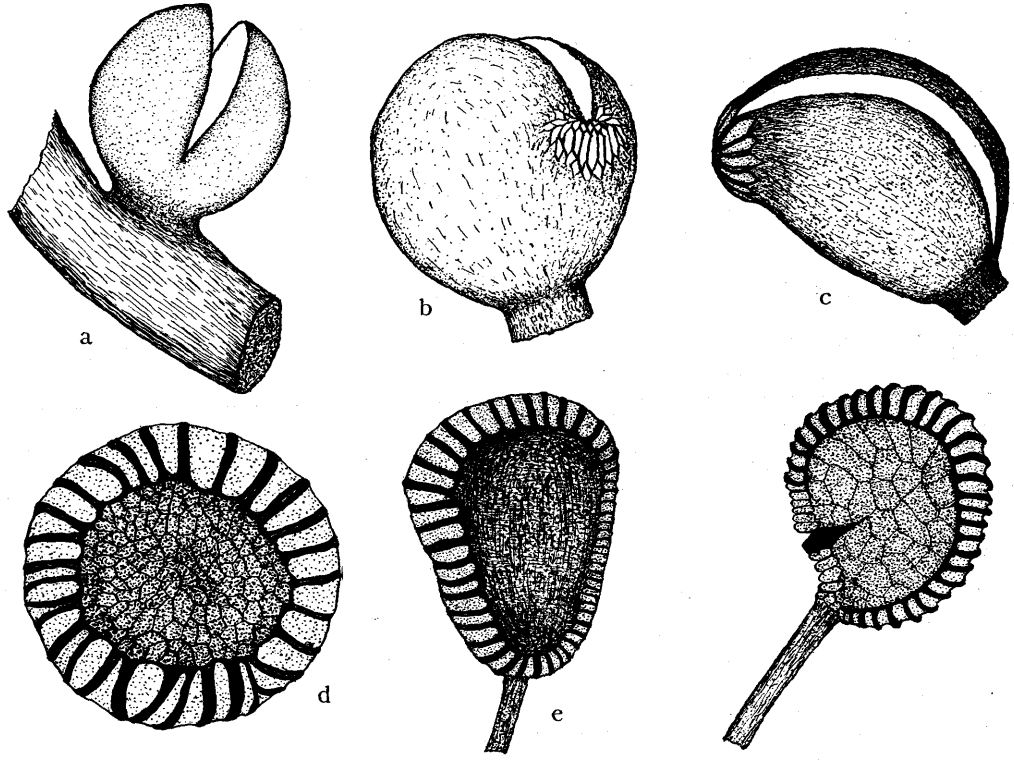

Fig. 2. Orthogenetic series in the evolution of a spore-throwing mechanism in the ferns. a, Sporangium of *Botrychium obliquum* Muhl. b, *Osmunda regalis* L. c, *Aneimia tomentosa* Sw. d, *Gleichinia longissima* Blume. e, *Cibotium chamissoi* Hk. & Bkr. f, *Onoclea sensibilis* L.

cylindrical stems to more and more flattened-stem forms, until in *R. elliptica* Lundb. and *R. russellii* Britt. and Rose the joints are very flat and thin.

Even the evolution of the mycorrhizal inter-relationship of fungus and root may show an orthogenetic series. J. Ramsbottom[1] in his study of mycorrhiza in the heaths says: "In the root-tip region we get an ascending series in the amount of fungus present from *Chimaphila umbellata* where the epidermal cells of some roots are without hyphae and other roots with hyphae, but not in every cell, to *C. maculata* with a greater number of the epidermal cells filled with hyphae; in *Pyrola rotundifolia* and *P. elliptica* all the cells are infected and there is the beginning of intertwined hyphae round the root tip; then in *Monotropa hypopitys* an increase in the width and extent of the sheaths and a division into two zones—an outer loosely woven mass of hyphae and an inner more compact one—and finally in *M. uniflora* a still greater width of the fungal sheath. In the least saprophytic species the epidermis soon dies off, carrying with it the fungal hyphae as in Chimaphila and Pyrola, whereas in Monotropa, especially *M. uniflora*, the epidermis is still living and filled with hyphae when the root is quite old. Corresponding with this increase in saprophytism there is an increase in the number of seeds produced and a reduction in their size and structure." It will be noted that a loss of chlorophyll is also involved in the more advanced species and that the simplification of the plant body and inflorescence and leaf structures attain their extreme limit also in *M. uniflora*.

AN ORTHOGENETIC SERIES LEADING TO A HIGHLY PERFECTED MECHANISM OF NO SURVIVAL VALUE TO THE INDIVIDUAL

The ferns have evolved a series of sporangia which represents a progression toward perfection in a mechanism which throws out the mature spores suddenly, by means of a hygroscopic ring of cells around the sporangium. The extreme type represents a very efficient and elaborately perfected structure which does the plant no good, for those species which are at the bottom of the series are just as successfully distributed as those with the perfected mechanism. Such a series is illustrated in Fig. 2. *Botrychium obliquum* Muhl. has a

[1]Ramsbottom, J. Trans. British Mycol. Soc., **8**: 28–61. 1923.

sporangium which merely opens by a simple slit and the spores fall out by accident (a). In *Osmunda regalis* L. the sporangium is nearly the same shape, also with a vertical slit, but at one side at the end of the dehiscence slit there is a peculiar group of cells with thickened walls (b). This group of cells represents the first step in the evolution of a remarkable structure, the annulus. So far as spore scattering is concerned, *Botrychium* can scatter its spores just as readily as *Osmunda* with the special patch of cells in the wall of the sporangium. In *Aneimia tomentosa* Sw. there is a decided advance in the group of thick-walled cells over that in *Osmunda* and is now arranged in the form of a ring at one end of the sporangium, the dehiscence still being by a vertical slit (c). In *Gleichinia longissima* Blume the sporangium has a complete ring of highly specialized cells (d). The figure represents a sporangium from the top. In *Cibotium chamissoi* Hk. and Bkr. there is also a complete ring which passes vertically around the sporangium to one side of the stalk (e). The cells on one side of the ring are much more elaborately developed than on the other. This sporangium is approaching the ideal type developed in the Polypodiaceae. In *Onoclea sensibilis* L. and many other Polypodiaceae there is a highly evolved incomplete ring with special lip cells on one side and cells with extremely hygroscopic walls on the other (f). When the sporangium is mature the hygroscopic ring, by turning back and straightening out, tears the sporangium open gradually but quickly and then suddenly collapses again with a jerk, thus throwing out the spores. A more perfect and ingenious mechanism for the purpose, and with the limited material employed, can hardly be imagined; but this perfected spore thrower is of no importance to the fern in giving it any advantage in distribution or survival. *Botrychium virginianum* (L.) Sw. is just as widely distributed and just as abundant if not more so, as *Onoclea sensibilis* L. It will be noted also that *Onoclea* has the pinnules which bear the sporangia rolled up into berry-like segments, which although they open up at maturity nevertheless must interfere decidedly with the scattering of the spores by the annulus mechanism. In the Hawaiian fern, *Cibotium chamissoi* Hk. and Bkr. the indusium forms a thick-walled box-like two-lobed structure with one lobe forming an open valve or lid for the other which holds the cluster of sporangia. Although the lid of the box opens up at maturity, this highly developed indusium must interfere decidedly with

the free discharge of the spores in the same way as the enrolled pinnule of *Onoclea*. At best, even with no special obstruction, the spores can be thrown only a short distance and their wide distribution is accomplished by wind, water and animals, which carry the spores of ferns like Botrychium without any throwing device as effectively and as widely as those with the perfected spore-throwing mechanism. The highly elaborated spore-throwing sporangium then is of no advantage to the plants which possess it but simply represents the end product of a perfective, evolutionary, orthogenetic series which came to perfection through intrinsic processes and causes.

SOME SIMPLE ORTHOGENETIC SERIES OF ANIMALS

Plants and animals form one organic system and the laws of heredity and evolution are the same fundamentally for both kingdoms. Since the higher plants are simpler in their organography and anatomy and especially since most plants have indeterminate and repetative growth, they are more convenient and reliable for the discovery of the true nature of heredity and evolution in general than the animals with their rapidly determinate ontogeny, which in all the higher forms do not give rise directly to new individuals by a normal process of budding and continuous growth as is common in plants. However, when one examines series of related animal species, either in the paleontological record or by a comparison of living forms, one finds on every side the same kind of orthogenetic series in the evolution of organisms and tissues as in plants. A few examples will be considered below for comparison with plant series. The presence of orthogenetic series was first studied intensively by paleontologists who could not escape the very clear cases presented by the degrees of coiling of Cephalopod shells, the development of complexity of the sutures in the shells of Ammonoids, the progressive change in the feet of the ancient horse series, the progressive evolution of the cusps of the teeth of mammals, and numerous other paleontological problems of a similar nature.

The Lamellicorn Beetles (Scarabaeidae) have a peculiar backward-projecting horn on the head or thorax which is evolved in various lengths in different species. *Canthon laevis* has no horn on the head or thorax. In *Copris tullius* the female has a short tubercle on the head and the male has a short horn. In *Xyloryctes satyrus* the female has a slight point on the head

and the male has a horn of medium length. In *Copris arizonensis* the female has a short spatulate horn on the head and the male has a prominent horn. In *Phanaeus carnifex* the female has a short blunt tubercle on the head while the male is provided with a long curved horn. In *Phanaeus quadridens* the female has a short blunt point on the head while the male has a very long horn. So all the horns of the males of these beetles and their relatives form a close orthogenetic series of lengths which give no advantage to the individual possessing the one type or another. The notion of special adaptation is not to be entertained rationally. The sex dimorphism present in these species was not originated because the female delights in a mate with long horns or because he can protect her and himself but because the two sexes are on a different metabolic level. Exactly similar phenomena can be observed between male and female structures in plants. Thus in the monecious *Zizania aquatica* L. the staminate spikelets are awnless while the carpellate spikelets have long awns.

The long-horned Wood-boring Beetles (Cerambycidae) as well as many other groups of insects present an orthogenetic series in the lengths of their antennae. *Moneilema varolare* and *Xylotrechus colonus* have rather short antennae, considerably shorter than the body. *Acanthocinus spectabilis* and *Monochamnus notatus* have antennae much longer than their bodies. Other long-horned wood-boring beetles take their positions in this series with all sorts of lengths of antennae. These various lengths are of no special value, but after the beetle has antennae of a given length it, of course, must accommodate its life and movements to the restrictions, advantages, or disadvantages of the length possessed or be eliminated in the struggle if the given length has any determinate effect, which seems improbable since the whole series of lengths has proven successful.

Among the important structures present in some groups of moths is the proboscis which also comes in series from zero to a structure of great length in the hawk moths (Sphingidae). The proboscis consists of the greatly lengthened maxillae and is useful for sucking nectar from flower cups and spurs. The lowest types of moths do not have a sucking proboscis. In *Sabatinca* sp. (Micropterygidae) the mandibles are functional dentate organs. In *Eriocrania* sp. (Micropterygidae) the mandibles are non-dentate and the terminal joint of the galea of either side is opposed to that of its fellow, thus exhibiting

the first step in the formation of a proboscis. In some forms of the Sphingidae the proboscis is also represented by a pair of tubercles, which is usually considered as representing a reduced condition, but there is no evidence that it was ever derived from an originally highly evolved proboscis. Now from these primitive conditions there are moths with proboscis of all sorts of lengths. *Protoparce quinquemaculata*, the common tomato-worm moth, has a proboscis 5–6 inches long. In *Cocytius proboscis* the proboscis is said to attain the enormous length of 10 inches. Here then is a remarkable orthogenetic series of lengths of an essential organ which runs parallel with various series of lengths of corolla tubes and spurs. Of course, it is evident that the moths with the longest probosces can sip nectar from the longest flower tubes and spurs, but they can and do also gather the nectar from flowers with comparatively short tubes. And such flowers are much more common in all areas than those with very long tubes. Thus the long proboscis has not evolved thru any adaptive necessity, and as stated above the flower with long tubes and spurs will be pollinated by the general swarm of pollen and nectar eating insects whether they are lucky enough to reach the nectar or not.

In various groups of wasps the thorax is separated from the abdomen by a slender connective or peduncle. This extra-ordinary structure which separates the front end of the body from the back end also comes in an orthogenetic series, as might be expected. In *Sphecius speciosus* the thorax and abdomen are contiguous. In *Chrysis ignita* there is no pro-longation of the connective but nevertheless a distinct separation of the thorax and abdomen. *Prionony x atrata* has a short connective. *Chlorion coeruleum* has a connective about one-half as long as the abdomen. *Eumenes petiolata* has a connective longer than the abdomen. *Ammophila sabulosa* has a con-nective about twice as long as the abdomen. To see any special advantage in such a condition is to proclaim one's self a firm believer in witch stories and fairy tales.

Mammals exhibit orthogenetic series in the lengths of their tails. Among the Ground Squirrels, the California Ground Squirrel (*Otospermophilus grammurus beecheyi*) has a tail 7 in. long. The Yukon Ground Squirrel (*Citellus osgoodi* has a tail 5–6 in. long. The Franklin Ground Squirrel (*Citellus franklini*) has a tail 5 in. long. The Apache Ground Squirrel (*Citellus spilosoma macrospilotus*) has a tail 3 in. long. Other

species of Citellus and other genera of ground squirrels have tails of various lengths which can all be arranged in orthogenetic series and have no relation to advantage or disadvantage to the animals in their various geographic regions and habitats.

The Lemurs live mostly in Madagascar. Their tails, which are never prehensile, show a very striking orthogenetic series. Three species which are nocturnal tree-dwellers have tails as follows: *Indrus brevicaudatus* has practically no tail. *Lepidolemur microdon* has a tail a little over one foot long. *Lemur fulvus* has a tail two feet long. There is no more reason for looking for an external cause as the driving force of evolution to explain the series of tail lengths of these animals than there is for looking for a driving force to explain the numerous series of compounds of organic substances outside of the atoms and particles that make up these compounds.

The tails of monkeys also represent orthogenetic series, from no external tail at all to very long appendages; and it will make no difference how we assume the series to have evolved, whether from short tails to long tails, from long tails to short tails, or from an original medium length tail in both directions, the fact of the series is still present and represents the result which the ultimate cause of the evolutionary movement has brought about, with no reference, directly, to utility or advantage or disadvantage in relation to survival. The Platyrrhines, which are exclusively New World monkeys, have various lengths of tails and some are prehensile and some are not. Some species in the family Cebidae have very short tails but more commonly the tails are long and often prehensile. In the genus *Cebus* the tail, though prehensile, is covered with hair to the tip, being thus a less perfect grasping organ than is the case with those monkeys which have a naked under surface to the prehensile end of the tail. This prehensile tail attains its greatest perfection as a "fifth hand" in the spider monkeys (Ateles), probably the most typically arboreal monkeys of America. Short-tailed American monkeys are species of the genus *Brachyurus*. So these monkey tails form orthogenetic series both in respect to lengths and also in respect to perfection as prehensile organs, from no prehensibility through various degrees to the extremely perfected prehensile tails of the spider monkeys. But these spider monkeys, being of comparatively light weight and slender build, should have the least use for these useful appendages in comparison with various other

more robust and heavy arboreal monkeys which have no prehensile tails whatever. The spider monkeys with their long legs and their perfected prehensile tails may be compared with the long-armed agile gibbons, like *Hylobates agilis*, which have no tails at all but which are among the most extreme of arboreal apes.

Now when one studies the Catarrhines, which are exclusively Old World monkeys, he finds no prehensile tails whatever, although they climb about on the trees just as the American monkeys do. These Catarrhines have tails of all sorts of lengths also making typical orthogenetic series from no external tail at all to some with very long tails. Thus *Presbytes melalophos*, the Simpai of Sumatra, has a tail nearly 3 ft. long, while the body of the animal is only about 1½ ft. long. *Cercopithecus diana* of Africa also has a very long tail. *Cercopithecus petaurista*, the White-nose Monkey of Western Africa, has a tail nearly 2 ft. long with a body measuring 15–16 in. *Cynocephalus mormon*, the Mandrill, has a short erect tail. *Cynopithecus niger*, of Celebes, has a very small rudimentary tail. *Macacus inuus*, the Barbary Ape of North Africa, has no external tail, and as stated above, the Agile Gibbon, an extremely active, arboreal species, also has no external tail. If the monkeys tails were originally long, why is there an orthogenetic series of lengths to complete disappearance in these Catarrhines when it is never of use as a grasping organ? Why did some of the American monkeys develop the prehensile ability while the old world monkeys acquired no such mechanism? Would a confirmed teleologist come to the conclusion that the American tropical forests were continuously subject to violent storms which made prehensile tails necessary while the Old World tropics were regions of perpetual calm which thus did not require the tree dwellers to evolve this "fifth" hand to keep from being hurled to earth and untimely death by "unkind mother nature?" The facts must be faced in their generality to see the real absurdity of the teleological explanations, whether Lamarckian or Darwinian. After a certain mechanism has evolved it may be of use to the organism but it could not be of special use until it had evolved to a rather decided stage of perfection. Imagine a poor, Old World monkey trusting for safety to his tail! This notion of adaptation is largely (in this case) a fairy tail. The tails are just not adapted to the trees. But it is remarkable how extremely some biologists are obsessed by the notion of *special adaptation.*

GENERAL CONCLUSION

The fact of orthogenetic series, both accumulative and perfective, plainly shows that the notions of specific adaptation and teleological causation have no scientific basis; since these series have no general correspondence with differential environments nor with any advantage to the individual. It is also clearly evident to the careful student of taxonomy in relation to evolution that the recognition of a perfective principle does not at all require the postulation of an entelechy as elaborated by Driesch and others. But the recognition of the orthogenetic series and of the perfective series as a result of the perfective principle in the organic kingdom does require us to recognize an internal creative principle which is just as evident and unescapable as the fact of the general atomic series and the complicated molecule systems of the chemist.

In addition to the evidence from orthogenetic series, further knowledge of the nature of the evolutionary process may be obtained from a study of the constancy attained at the limits of the series. This unchangeableness is well illustrated by the 4,000 species of grasses all of which have attained the two-ranked condition of the leaves and the unilocular ovulary. Both of these characteristics represent the possible determinate evolutionary limit. The same is true for the ten to fifteen thousand species of the subfamily Orchidatae, practically all of which have two-ranked leaves and also have a unilocular ovulary and a single stamen always occupying the same position in the flower. This constancy of the evolved structures which have attained the limit of the orthogenetic series shows how far from the mark are those speculations which see in the abnormal mutations caused by X-rays, radium, ultra-violet light, cosmic rays, etc., the fundamental cause of the evolution of the taxonomic system of plants and animals. The grasses and orchids and other such large culmination groups have been bombarded for millions of years by cosmic and other rays but the fundamental potentialities remain unchanged, although an enormous amount of subordinate evolution and speciation has been going on.

In recognizing the existence of an *internal* creative principle, science comes to its limit. The next step in causative reasoning, as to what is the ultimate cause of this orthogenetic, progressive, perfective principle, is a question of theistic philosophy and belongs to the domain of the philosopher rather than the

scientist. An anarchistic philosophy is definitely contradicted by the facts of the orderly taxonomic system in general and by the presence of the perfective, orthogenetic series in particular. The biologist, however, can recognize the fact of a *universal design* in nature as a scientific discipline and the remarkable success which the fundamental evolutionary activities have brought about in the *balance of nature*, which not only permits thousands of the most diverse types and species to come into existence but also allows, in spite of the struggle for life, endless numbers of species to continue successfully in the narrow shell of the earth's surface for millions of years.

The examples of orthogenetic series discussed in this paper, and which could be multiplied indefinitely, show again that evolution is intrinsic rather than extrinsic, kinetic rather than static; progressive, orthogenetic, and perfective rather than haphazard; and finally determinative in many of its characteristic movements.